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Plant response to solar ultraviolet-B radiation in a southern South American *Sphagnum* peatland

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Summary

1 Plant growth and pigmentation of the moss *Sphagnum magellanicum* and the vascular plants *Empetrum rubrum*, *Nothofagus antarctica* and *Tetroncium magellanicum* were measured under near-ambient (90% of ambient) and reduced (20%) ultraviolet-B (UV-B) radiation for three growing seasons in a *Sphagnum* peatland in Tierra del Fuego, Argentina (55° S).

2 Reduction of solar UV-B increased height growth but decreased volumetric density in *S. magellanicum* so that biomass production was not influenced during the 3 years. The morphology of vascular plants tended not to respond to UV-B reduction.

3 A 10–20% decrease in UV-B-absorbing compounds occurred in *T. magellanicum* under solar UV-B reduction. No effects were seen on chlorophyll or carotenoids in *S. magellanicum*, although, for UV-B-absorbing compounds, a significant interaction between UV-B and year suggests some response to solar UV-B reduction.

4 The climate-related growth of the dwarf shrub *E. rubrum* was assessed retrospectively by correlating an 8-year record of annual stem elongation with macroclimatic factors including solar UV-B and visible radiation, precipitation and temperature.

5 No significant negative correlations were found between annual *E. rubrum* stem elongation and ambient solar UV-B, the ratio of UV-B : visible radiation, or the 305-nm : 340-nm irradiance ratio for an 8-year record (1990–91 to 1997–98), nor was stem elongation affected by solar UV-B reduction in our experimental field plots after 3 years.

6 The role of solar UV-B radiation on plant growth in *Sphagnum* peatlands in Tierra del Fuego, Argentina, is likely to depend on the severity of stratospheric ozone depletion over the next several decades. The increases in ambient solar UV-B associated with ozone depletion over the last 20 years are less than the difference between our radiation treatments. Therefore, providing that the ozone layer substantially recovers by the middle of this century, only modest effects of increased solar UV-B on plant growth may be expected.

Key-words: Antarctic ozone hole, peatland, Tierra del Fuego, ultraviolet radiation, UV-B

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Introduction

The number of days of pronounced ozone depletion over Tierra del Fuego (55° S), Argentina, during the austral spring has increased greatly over the last two decades due to the passage of the Antarctic 'ozone hole' over the southern tip of South America (Rousseaux *et al.* 1999). Substantial ozone depletion is also apparent in the summer months, and is likely to be related to the general deterioration of the ozone layer in the Southern Hemisphere (Frederick *et al.* 1994; Rousseaux *et al.* 2001). Dramatic increases in daily solar ultraviolet-B radiation (UV-B, 280–320 nm) reaching the Earth's surface in this area often occur when the 'ozone hole'

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remains over Tierra del Fuego for periods of several days (Bojkov *et al*. 1995; Kirchhoff *et al*. 1997). Trends in monthly solar UV-B based on ground-level measurements are much more difficult to detect due to prevalent cloud cover over Tierra del Fuego and Antarctica (Díaz *et al*. 2000). Nevertheless, relative to the late 1970s, terrestrial ecosystems in Tierra del Fuego (55° S) often receive increased UV-B throughout the spring and summer months (Frederick *et al*. 1994). Such increases in ultraviolet intensities due to ozone depletion can be measured as far north as New Zealand (45° S) (McKenzie *et al*. 1999).

The greater severity of ozone depletion over high latitudes in the Southern Hemisphere than for similar latitudes in the Northern Hemisphere has led to several recent field studies of plant responses to solar UV-B radiation. In the native perennial herb *Gunnera magellanica* midday DNA damage correlated well with ambient solar UV-B during the austral spring in Tierra del Fuego (Rousseaux *et al*. 1999) and experimental manipulations indicated that solar UV-B also reduced leaf expansion and increased insect herbivory (Rousseaux *et al*. 1998; Rousseaux *et al*. 2001). Species of *Nothofagus* dominate the forests of Tierra del Fuego and other areas of southern Argentina and Chile. In New Zealand, seedlings of the southern beech, *Nothofagus solandri*, exhibited changes in plant architecture due to solar UV-B manipulations (Hunt & McNeil 1999). On the Antarctic Peninsula, solar UV-B reduction greatly increased leaf growth of the tussock grass *Deschampsia antarctica* over 4 years, but the cushion-forming *Colobanthus quitensis* was affected to a lesser degree (Day *et al*. 1999, 2001). Treatments in these Southern Hemisphere studies employed solar UV-B reduction rather than UV-B supplementation because UV-B levels are already elevated relative to historic values.

At high-latitude sites in the Northern Hemisphere, UV-B supplementation using special UV fluorescent lamps has been employed to simulate the increase anticipated with ozone depletion. Some reductions in stem elongation, as well as changes in herbivory, decomposition and reproductive output were seen under supplemental UV-B for several dwarf shrub species in a heathland ecosystem at Abisko, Sweden (68° N), after two to four growing seasons (Gehrke *et al*. 1995; Johanson *et al*. 1995; Gwynn-Jones *et al*. 1997; Phoenix *et al*. 2000). However, very few effects on stem elongation were apparent after seven growing seasons, although interactions with precipitation treatments were more common (Phoenix *et al*. 2001). The growth of potted mountain birch seedlings (*Betula pubescens*) native to these same Swedish heathlands was not affected by supplemental UV-B radiation in an outdoor study (Weih *et al*. 1998).

The influence of UV-B radiation has been examined less for bryophytes than it has for vascular plants. Bryophytes are critical components of many polar and subpolar ecosystems because of their capacity to retain nutrients and water, and their role in carbon accumulation in peatlands (Oechel & Van Cleve 1986). The subarctic mosses *Hylocomium splendens* and *Polytrichum commune*, which form part of the understorey in subarctic heathlands, showed reduced annual length increments in a 3-year study under supplemental UV-B (Gehrke 1999), although some growth parameters in *H. splendens* actually increased in a longer-term study (Phoenix *et al*. 2001). *Sphagnum fuscum*, a hummock-forming species that commonly dominates many peatbogs in the Northern Hemisphere, had reduced height growth under supplemental UV-B during two growing seasons (Gehrke 1998), but its biomass production was not affected. After one growing season, attenuation of solar UV-B in a *Sphagnum* peatland in Tierra del Fuego, Argentina, affected neither height growth of the cosmopolitan *Sphagnum magellanicum* nor the vascular plant species (Searles *et al*. 1999). *Sphagnum* grows around, and sometimes over, vascular plant stems in many peatlands, and any UV-B effects on the growth of either component may therefore have long-term effects on bog plant communities and ecosystem function.

The objectives of this 3-year field study were to: (i) assess the role of solar UV-B for the growth and pigmentation of *Sphagnum* moss and associated vascular plants in long-term field plots in a *Sphagnum* peatland under two different UV-B levels; and (ii) investigate retrospectively whether the stem elongation of *Empetrum rubrum*, a dwarf shrub found in our long-term *Sphagnum* plots, exhibited any negative correlations with ambient solar UV-B over an 8-year period. Morphological indicators of annual growth have been used for other dwarf shrubs and mosses to evaluate growth related to historical climate records (Callaghan *et al*. 1989, 1997).

Materials and methods

EXPERIMENTAL SITE

Our experimental site is 20 km west of the city of Ushuaia (55° S) on Isla Grande in the Province of Tierra del Fuego, Argentina. The general vegetation types include deciduous *Nothofagus (* southern beech) forest, with *Sphagnum* and *Carex* peatlands lying in the mountain valleys and along the coast, and some shrub-steppe communities in disturbed habitats. The field plots are located in a *Sphagnum* peatland adjacent to a small lake (Laguna Negra) in the Parque Nacional Tierra del Fuego. Cover of *Sphagnum magellanicum* Brid. is nearly 100% and the prominent vascular plants emerging from the *Sphagnum* peat are small *Nothofagus antarctica* (Forster f) Oersted (a deciduous southern beech tree), *Empetrum rubrum* Vahl ex Willd. (an evergreen dwarf shrub), and *Tetroncium magellanicum* Willd. (a rhizomatous perennial monocot). These emergents usually extend less than 30 cm above the moss layer. The pH and the vascular plant vegetation

of this peatland suggest that it is minerogenous (i.e. water inflow mostly from nutrient-rich groundwater) and in an early successional stage towards becoming a raised, ombrogenous peatland (i.e. water and nutrient inflow mostly from precipitation) (Mataloni 1999; Searles, personal observation). Annual precipitation and temperature are 525 mm and 5.5 °C, with precipitation distributed fairly evenly throughout the year (Food and Agriculture Organization 1985).

EXPERIMENTAL SET-UP AND TREATMENTS

Twenty experimental plots of 1.4×2.0 m were established in February and March 1996, and a boardwalk was constructed to avoid damaging the vegetation and altering the hydrology around the plots. The experimental UV-B manipulations were initiated in October 1996 during the austral spring and maintained in the plots for three growing seasons (1996–97, 1997–98 and 1998–99) from October until early to mid-March (autumn). Ambient solar UV-B had decreased to very low levels by mid-March and leaf senescence was occurring. The plots were covered by snow for most of each winter, and the treatments were reinitiated in the spring 2–3 weeks before bud break of *N. antarctica*. Measurements of the moss *S. magellanicum* indicated that minimal or no growth occurred in the plots during the fall and winter.

Using a completely randomized design, 10 of the plots were covered by clear 38 μm thick 'Aclar' plastic film (type 22 A, Honeywell, formerly Allied Signal, Pottsville, Pennsylvania, USA) to provide near-ambient UV-B radiation. The other 10 plots were covered by 100 μm extra-clear polyester plastic (optically equivalent to 'Mylar-D', DuPont Co., Wilmington, Delaware, USA) to provide a reduced solar UV-B level. Both filters were perforated using an electric hot-wire melter that formed a pattern of slits (slit size: 2×30 mm) orientated perpendicular to each other and covering 8% of the plastic film to allow for a partial, rather than complete, attenuation of solar UV-B. The slits also formed a matrix of louvres that allowed rainfall to pass through the plastic filters.

Ultraviolet-B radiation transmittance of the perforated films was measured using the SUV 100 scanning double monochromator (Biospherical Instruments, San Diego, California, USA) in Ushuaia, Argentina, and in Logan, Utah, using an Optronic 742 double-grating spectroradiometer (Optronic Laboratories, Orlando, Florida, USA). The instrument in Ushuaia is part of the US National Science Foundation UV Radiation Monitoring Network (Booth *et al*. 1994), and the spectroradiometer in Logan has been previously described by Flint & Caldwell (1998). Measurements were taken on 12 February 1997 in Ushuaia under mostly cloudy skies and in Logan on both sunny and cloudy days at a midday solar elevation equivalent to that of Ushuaia at the summer solstice (21 December). Some measurements were done in Logan because the implementation of an increased scanning protocol at the Ushuaia monitoring station did not allow sufficient time for our scans. During measurements at both locations, instantaneous photon flux density (PFD, 400–700 nm) was monitored using a quantum sensor (LiCor, Lincoln, Nebraska, USA) to assess the stability of cloud cover over the duration of the scan. The quantum sensor was also used to evaluate PFD transmission through the perforated filters. All of the above measurements were performed 15–20 cm below plastic films that were approximately the same size as the plastic films over the field plots. At the field plots, the films were horizontally suspended 35 cm above the ground surface and 10 cm above the tallest vegetation. The plastic filters were inspected every 2–3 days and replaced if damaged by the wind. All filters were replaced during the middle of the season. Measurements of UV absorbance in a spectrophotometer did not indicate any photodegradation of either the clear polyester or the Aclar.

To compare the radiation environment at the Laguna Negra field site relative to the UV monitoring station in Ushuaia 20 km away, ambient solar UV and visible radiation were monitored every 15 min at Laguna Negra during the second and third field seasons using three broadband UV sensors with a spectral sensitivity mimicking the erythemal action spectrum (Model PMA2102, Solar Light Co., Philadelphia, Pennsylvania, USA) and a quantum sensor. Daily differences between the two locations were primarily related to cloudiness, and differed by no more than 2% over an entire season. Thus, the measured values of UV and visible irradiance in Ushuaia are relevant to our field site.

Sphagnum moisture content and air temperature were periodically measured within the field plots. The moisture content of the *Sphagnum* capitula (the top centimetre of the shoot) inside the plots indicated no apparent differences under the two types of plastic film throughout the growing season. Moisture content of the *Sphagnum* outside of the plots was similar to the values measured inside the plots. No differences in air temperature could be detected inside and outside of the plots, most likely due to the persistent winds, whose average monthly speeds are near $5\ m\ s^{-1}$. Further details of the temperature measurements can be found in Searles *et al*. (1999).

PLANT GROWTH MEASUREMENTS

Plant morphological measurements were taken for the *Sphagnum* moss and emergent vascular plants in each of the three growth seasons during the late spring and summer. To measure the height growth of *S. magellanicum*, six stainless steel cranked wires were installed in each plot in October 1996 using the method of Clymo (1970). This method involves using stainless steel wires (shaped like the handle of an old-fashioned car-starting crank) as reference markers, with one end pushed

vertically into the *Sphagnum* carpet, a short horizontal section level with the *Sphagnum* surface, and the other end projecting vertically upward above the surface. Two more cranked wires were added both inside and outside of each plot in October 1997. Height growth was measured each year during mid-January and in late February to early March. To assess biomass production and volumetric density of *S. magellanicum* over the 3 years of the study, six sections (5 × 5 cm) of the moss carpet from each plot were harvested at the exact locations of the original six cranked wires (where yearly *Sphagnum* height growth was measured) near the end of the third growing season in late-February 1999. The number of *S. magellanicum* stems was counted in the 3 × 3 cm interior of each section and seven of these stems were cut into segments corresponding to the biomass for the first year and for the second and third years combined. The second and third years of moss growth were not separated due to concern about the error associated with bisecting these two layers. It was assumed that minimal biomass had been lost from moss grown in the first and second years due to decomposition, leaching or other factors. The *S. magellanicum* segments were dried at 60–70 °C for 72 h and weighed. Volumetric density (g dm^{-3}) was calculated for each age using the number of *Sphagnum* stems in the 3 × 3 cm sample, the average dry mass of a moss segment and the height growth measured from the cranked wires. Biomass production (g m^{-2}) was also determined.

For the vascular plants, the yearly stem elongation of *E. rubrum* was measured in eight stems per plot during mid-January of the third year using innate yearly growth markers (bud scales) to give values for all three growing seasons. These stems were then harvested for yearly biomass determinations and a later counting of leaf number. Stem length in *N. antarctica* was measured twice each season on six stems per plot marked at the beginning of each growing season. Leaf number and leaf length were also measured in *N. antarctica* twice during each of the second and third seasons. Leaf length was measured on two leaves that had recently expanded. For *T. magellanicum*, leaf elongation was measured on 10 leaves per plot for two sets of marked leaves during the spring (when most leaf elongation occurs) of the second and third growing seasons. The initial leaf blade length (approximately 10 mm) of young *T. magellanicum* leaves was recorded and then re-measured after 2 weeks as the leaf was nearing its full length.

PIGMENTATION

Carotenoids, chlorophylls and UV-B-absorbing compounds were determined for *S. magellanicum* similarly to Searles *et al*. (1999). Briefly, pigments from the top 5–6 mm of *Sphagnum* stems were extracted in 5 mL of 100% methanol heated to 60 °C for 10 min. Ultraviolet-B-absorbing compounds of *S. magellanicum* were also extracted in 5 mL of 1-M NaOH at room temperature for 48 h based on the method of Schnitzler *et al*. (1996). This additional method was employed due to a suspected large component of wall-bound phenolics in the moss. No strong shift in absorbance (measured in a spectrophotometer) in these crude NaOH extractions from shorter to longer UV wavelengths was noticed when compared with methanol extractions, although subtle changes in the absorbance curves could have been missed. The sampling for the pigments of *S. magellanicum* was performed annually in mid-February or early March. For UV-B-absorbing compounds and anthocyanins in the vascular plants, leaves from the current year's growth of each species were extracted in a 99 : 1 MeOH : HCl solution and stored at –20 °C similar to Beggs & Wellmann (1985). These samples were taken each year in mid-February to early March. Absorbance in a spectrophotometer was used for the measurement of all pigment extractions. After these measurements, the *Sphagnum* and vascular plant leaf samples were dried at 60–70 °C for 48 h and then weighed for the expression of absorbance on a dry mass basis to correct for any differences in the amount of *Sphagnum* or vascular leaf tissue used in the extractions. No determinations of chlorophyll or carotenoids were made in the vascular species.

RETROSPECTIVE ASSESSMENT OF *E. RUBRUM* GROWTH

The growth of *E. rubrum* in *Sphagnum* peatlands was assessed by correlating an 8-year record of *E. rubrum* stem elongation with climatic factors, including daily integrated solar UV-B and visible radiation, daily temperature and monthly total precipitation. Irradiance ratios of solar UV-B : visible radiation and 305-nm : 340-nm radiation were also compared with stem elongation. The 305 : 340 nm ratio provides an indicator of ozone depletion because the transmission of 305 and 340 nm to the Earth's surface is similarly affected by cloudiness, while the two wavelengths have markedly different coefficients of absorption by ozone (Frederick *et al*. 1994). The climatological values used for the correlations with stem elongation were from the early spring (October), early summer (December) and the overall growing season (October to February). The early spring was chosen *a priori* because ozone fluctuations associated with the Antarctic 'ozone hole' are the most pronounced at this time. The early summer was chosen because solar radiation is greatest during this period.

The 8-year record of *E. rubrum* stem elongation included the growing seasons from 1990–91 to 1997–98. In total, 182 stems growing in *S. magellanicum* were collected in October and November 1998 from four *Sphagnum* peatlands, with 40–50 stems collected from each of three peatlands in the Parque Nacional Tierra del Fuego and a peatland in the Valley of Andorra near the city of Ushuaia. The Laguna Negra site with the

experimental field plots was not included as one of the sites due to the amount of standing water in the peatland at the time of sampling. Annual stem elongation was measured in the laboratory using calipers. The solar radiation data were provided by the US National Science Foundation UV monitoring station and the temperature and precipitation data were recorded by the Centro Austral de Investigaciones Cientificas (CADIC) in Ushuaia.

STATISTICAL ANALYSIS

To assess potential differences in plant response between the near-ambient and reduced UV-B levels, growth and pigmentation parameters were analysed separately for each species using analyses of variance. Repeated-measures analyses of variance were employed in most instances with UV-B and year as fixed-effects factors, and with plots and repeated measurements on plots as the random-effects factors. A three-way factorial was incorporated as a split-plot-in-time design for *T. magellanicum* and *N. antarctica* growth parameters, with UV-B, year and season (or month) being the three fixed-effect factors, and with plots and repeated measurements on plots again being the random-effects factors. The effects of UV-B were also determined for each year in all analyses. To avoid pseudoreplication, the plot was considered the experimental unit for the UV-B treatment rather than individual plants or stems within plots. Computations were performed using PROC MIXED in SAS Release 6.12 (SAS Institute Inc., Cary, North Carolina, USA).

For the retrospective assessment of *E. rubrum* growth, simple linear correlations were performed between annual *E. rubrum* stem length and climatic variables. The *E. rubrum* data from all four peatlands were combined for analysis because we were not interested in specific site differences. Results were considered to be statistically significant in this study only if the *P*-values were $P \leq 0.05$.

Results

SOLAR UV-B ENVIRONMENT

Detailed measurements of solar UV-B transmittance through the plastic filters were done to assess the influence of the perforations (2 mm × 30 mm slits) in the filters under different sky conditions; especially for the UV-B-absorbing filter, clear polyester (Fig. 1). Measurements of the perforated clear polyester near midday under cloudy conditions in Ushuaia, Argentina, revealed transmittance of around 17% at 300 nm. The UV-B transmittance at this wavelength of an unperforated polyester filter is near zero. For clear sky conditions, the percentage UV-B transmittance of the polyester was similar to that under cloudy skies based on measurements in Logan, Utah, USA. The transmittance of the polyester increases greatly with wavelength through the UV-A starting at 320 nm and is about 90% throughout the visible waveband (400–700 nm). The UV-B-transparent filter, Aclar, transmits 85–90% of UV and visible wavelengths. The somewhat lower measured transmittance of perforated clear polyester at 300 nm, but not at other wavelengths, in Logan relative to Ushuaia is most likely related to how the two different spectroradiometers measured the small amount of radiation present at 300 nm.

The measured daily integrated UV-B levels for each month during the growing season of our 3-year study are shown in Table 1. Given a UV transmittance at 300 nm of approximately 15–20% under the clear perforated polyester filters in Ushuaia (Fig. 1), biologically effective UV-B in the reduced UV-B plots was always less than 1 kJ m^{-2} d^{-1} when weighted by the generalized plant action spectrum (Caldwell 1971).

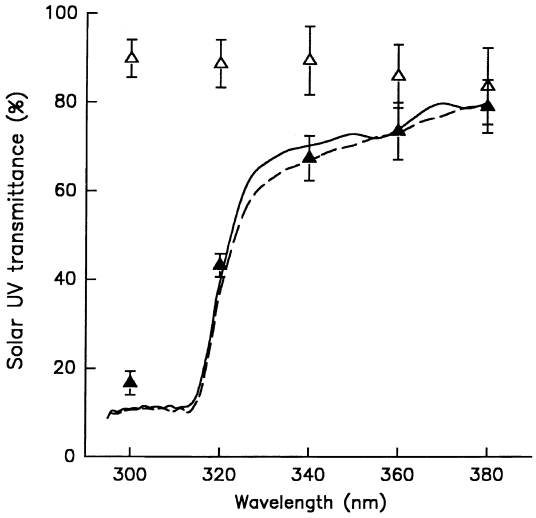

Fig. 1 Solar UV transmittance (%) through perforated clear polyester and perforated Aclar filters. Spectroradiometer scans (300–380 nm) were taken on 12 February 1997 under mostly cloudy skies in Ushuaia, Argentina, for the clear polyester (filled triangles) and Aclar (hollow triangles) filters. Measurements were only taken every 20 nm in Ushuaia. Means are shown ± the standard deviation. In Logan, Utah, USA, scans (295–380 nm) under perforated clear polyester were performed under both uniformly cloudy (solid line) and clear skies (dashed line) at a midday solar elevation equivalent to that of Ushuaia at the summer solstice (21 December).

Table 1 Measured monthly averages of daily integrated solar UV-B radiation during the growing season from 1996 to 1999 in Ushuaia, Argentina. The UV-B values (kJ m^{-2} d^{-1}) are normalized to one at 300 nm and weighted by the generalized plant action spectrum (Caldwell 1971). Means are shown ± the standard deviation among days for a given month

Month	1996–97	1997–98	1998–99
October	1.54 ± 0.54	2.24 ± 0.95	2.07 ± 1.14
November	3.89 ± 1.77	4.63 ± 1.36	2.96 ± 0.86
December	4.48 ± 1.39	4.08 ± 1.22	4.41 ± 1.61
January	3.82 ± 0.98	4.17 ± 1.22	4.58 ± 1.18
February	2.32 ± 0.59	4.03 ± 1.22	2.86 ± 0.90
March	1.60 ± 0.52	1.53 ± 0.52	1.48 ± 0.72

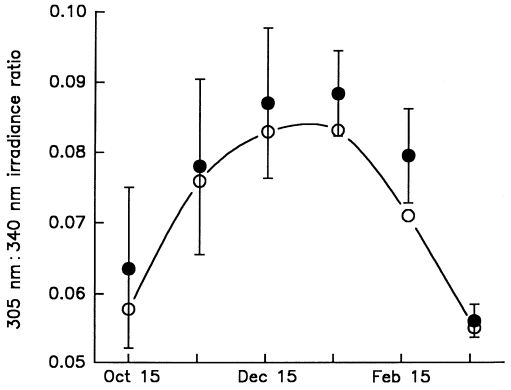

Fig. 2 Measured noon 305 : 340 nm irradiance ratios and model calculations. The solid line with hollow circles shows the model-calculated 305 : 340 nm ratios at noon (a sensitive indicator of ozone depletion) using monthly ozone values from 1980 to 1986. The point (filled circle) for each month represents the measured monthly average at noon from the UV monitoring station in Ushuaia (1989–1999). The error bars are the standard deviation among days for a given month.

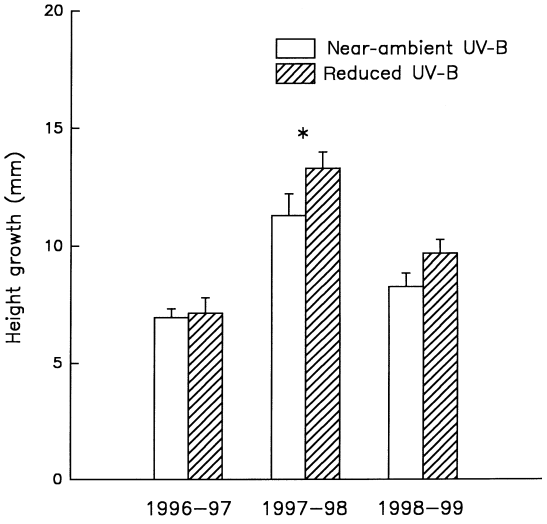

Fig. 3 The height growth of *S. magellanicum* during each of three growing seasons under near-ambient solar UV-B and reduced UV-B radiation treatments. n = 10 plots per UV-B level with means ± the standard error. *P = 0.02.

The near-ambient plots received 1.3–4.0 kJ m^{-2} d^{-1} depending on the month and growing season.

Ground-based measurements from the US National Science Foundation UV Monitoring Network station in Ushuaia show an increase of at least 10% in the noon 305 : 340 nm irradiance ratio (a sensitive indicator of ozone depletion that eliminates the effects of cloud cover) for most of the growing season during the 1990s compared with model values for 1980–86 (Fig. 2). The model values are calculated from satellite-based ozone values from the Total Ozone Mapping Spectrometer and the atmospheric transmission model of Frederick & Lubin (1988). Validation of the model has shown strong agreement between measured and calculated irradiances over Tierra del Fuego (Díaz *et al.* 1996). The averaged monthly ozone values from 1980 through 1986 were used to provide a baseline for stratospheric ozone values over Tierra del Fuego similar to Frederick *et al.* (1994), although some ozone depletion was already occurring by this time over this region.

PLANT MORPHOLOGY AND BIOMASS

The morphology of the moss *S. magellanicum* was affected by UV-B reduction (Figs 3 and 4). A significant increase (18%) in height growth in reduced UV-B plots relative to near-ambient UV-B plots was apparent during the second growing season (1997–98; P = 0.02). The results were qualitatively similar (i.e. a 17% increase) during the third growing season (1998–99), but not statistically significant (P = 0.07). Repeated measures analysis of variance indicated a P-value of 0.05 for height growth over the 3 years of the study. A decrease in volumetric density with UV-B reduction occurred during the second and third seasons (P = 0.04). The increase in height growth tended to offset the decrease in volumetric density under reduced UV-B such that biomass production was not influenced during the 3 years (Fig. 4). The *S. magellanicum* stem density under reduced UV-B (32 200 ± 7400 m^{-2}) and near-ambient UV-B (30 000 ± 5800 m^{-2}) was not significantly different. Based on cranked wires installed

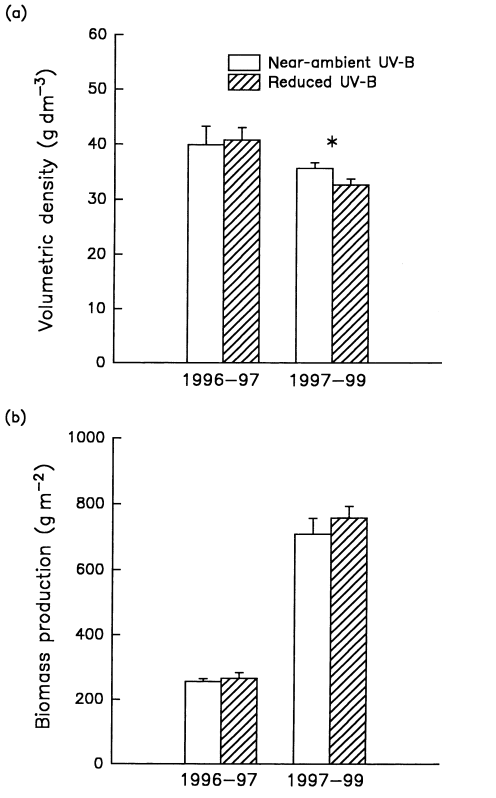

Fig. 4 The volumetric density (a) and biomass production (b) of *S. magellanicum* during the first growing season (1996–97) and the second and third growing seasons (1997–99) combined under near-ambient solar UV-B and reduced UV-B radiation treatments. The latter two seasons were harvested together to reduce error. n = 10 plots per UV-B level with means ± the standard error. *P = 0.04.

Table 2 Morphological measurements (vascular plants) and UV-B-absorbance values (moss and vascular plants) during the three growing seasons under near-ambient solar UV-B (+ UV-B) and reduced UV-B (– UV-B) radiation treatments. Absorbance (Abs. mg^{-1} at 305 nm for a 1-ml extract) was measured on a dry mass basis for acidified extracts except in *S. magellanicum* where sodium hydroxide extraction was used. n = 10 plots per UV-B level with means ± SE

		1996–97		1997 –1998		1998–1999	
Variable	Species	+ UV-B	– UV-B	+ UV-B	– UV-B	+ UV-B	– UV-B
Stem elongation (mm)	*Empetrum*	19.2 ± 1.6	18.7 ± 0.8	23.9 ± 2.2	22.9 ± 1.1	17.2 ± 0.9	16.2 ± 0.8
	Nothofagus	29.0 ± 2.4	25.4 ± 1.7	21.6 ± 1.8	22.1 ± 1.9	24.8 ± 3.3	25.3 ± 2.6
Leaf length or elongation (mm)	*Nothofagus*	–	–	8.3 ± 0.4	7.8 ± 0.5	8.8 ± 0.3	8.2 ± 0.4
	Tetroncium	–	–	19.3 ± 1.7	22.7 ± 1.0	17.8 ± 1.0	20.6 ± 1.0
UV-B-absorbing compounds	*Empetrum*	4.35 ± 0.20	3.96 ± 0.22	3.18 ± 0.17	2.67 ± 0.21	3.47 ± 0.14	3.07 ± 0.18
	Nothofagus	6.62 ± 0.53	6.79 ± 0.46	6.06 ± 0.38	6.04 ± 0.30	6.99 ± 0.44	6.48 ± 0.56
	Sphagnum	0.88 ± 0.04	0.99 ± 0.07	0.97 ± 0.03	0.92 ± 0.03	0.94 ± 0.04	0.90 ± 0.04
	Tetroncium	–	–	1.74 ± 0.07	1.54 ± 0.06	2.16 ± 0.08	2.03 ± 0.07

Table 3 The correlation coefficients between *E. rubrum* stem elongation and macroclimatic factors or irradiance ratios for the growing seasons 1990–91 to 1997–98. The months shown represent the spring, early summer, and the entire growing season

Months	UV-B	Visible	UV-B/visible	305/340 nm	Temperature	Precipitation
October	−0.07	−0.05	−0.05	−0.05	0.18	−0.25
December	0.22	0.76*	−0.17	−0.18	0.44	−0.64
October–February	−0.46	−0.15	−0.60	−0.15	0.24	−0.59

P = 0.03.

inside and outside of the plots at the beginning of the second growing season, height growth inside of the plots was not noticeably affected by merely having filters over the plots (data not shown).

Morphology of the vascular plants tended not to respond to solar UV-B reduction. The leaf elongation of *Tetroncium magellanicum* (the perennial monocot) was slightly greater with UV-B reduction during the spring of the second (P = 0.09) and third (P = 0.06) years, but there were no statistically significant treatment differences at P = 0.05 (Table 2). Leaf elongation for the first season in *T. magellanicum* was not sampled in the same manner, although the elongation was also somewhat greater with solar UV-B reduction (see Searles *et al*. 1999). In *Empetrum rubrum* (the dwarf shrub), there were no UV-B effects during the three growing seasons on number of leaves, stem length or above-ground biomass (Table 2 and data not shown). The stem and leaf morphology of *Nothofagus antartica* (the southern beech tree) was not affected by UV-B reduction.

PIGMENTATION

Leaves of the herbaceous *T. magellanicum* showed a decrease in UV-B-absorbing compounds at 305 nm under solar UV-B reduction during the second and third years of the study using repeated-measures analysis of variance (P = 0.05) (Table 2). The decrease in absorbance by leaf pigments in *T. magellanicum* was actually more apparent between treatments at 360 nm (2.63 ± 0.11 for + UV-B, 2.23 ± 0.10 for – UV-B; P = 0.004) than at 305 nm. In *E. rubrum*, a trend of decreased UV-B-absorbing compounds at 305 nm under solar UV-B reduction for each of the three seasons was not statistically significant (P = 0.08). In *N. antarctica* and *S. magellanicum*, the UV-B-absorbing compounds were also not affected, although an interaction between UV-B level and year occurred in the moss (P = 0.04). In the moss, crude extractions of UV-B-absorbing compounds with either acidified methanol or sodium hydroxide did not change the relative values between the treatments at 305 nm. Measurements of other pigments such as anthocyanins in *N. antarctica* and *E. rubrum* during the third growing season showed no effects of UV-B treatment nor did chlorophylls and carotenoids in *S. magellanicum* in any of the three growing seasons (data not shown).

RETROSPECTIVE ASSESSMENT OF *E. RUBRUM* GROWTH

Annual *E. rubrum* stem elongation did not show a significant relationship with ambient solar UV-B, the ratio of UV-B : visible radiation, or the 305 : 340 nm irradiance ratio for the 8-year record (1990–91 to 1997–98) (Table 3). Stem elongation for a given year was positively correlated with visible radiation (P = 0.03) for the month of December (early summer). This correlation is for visible radiation values from the same

year as the *E. rubrum* growth. Relationships between previous year's climate and *E. rubrum* stem elongation were not significant (data not shown).

Discussion

LONG-TERM CHANGES IN SOLAR UV-B RADIATION

A comparison of UV irradiance ratios calculated from satellite-based ozone column measurements with ground-based values in Tierra del Fuego, Argentina, indicated that, when variation due to cloud cover was removed, solar UV-B radiation increased during the spring and summer by at least 10–15% from 1980–86 to the 1990s (Fig. 2). A similar increase in UV-B has occurred over Lauder, New Zealand (45° S), in the summertime during the 1990s (McKenzie *et al*. 1999). These increases during the summer are most likely associated with the general decrease in stratospheric ozone in the Southern Hemisphere. The passage of the Antarctic 'ozone hole' over the southern tip of South America is more influential during the spring when distinct increases in solar UV-B associated with the 'ozone hole' have been demonstrated by many authors (e.g. Bojkov *et al*. 1995; Kirchhoff *et al*. 1997; Rousseaux *et al*. 1999).

PLANT PERFORMANCE UNDER REDUCED SOLAR UV-B

The morphological effects of reduced UV-B on the growth of the moss *S. magellanicum* in Tierra del Fuego are comparable with the effects of UV-B enhancement in *S. fuscum* in Abisko, Sweden (Gehrke 1998). Both studies showed UV-B effects on height and measures of volumetric density that offset each other, such that no changes in biomass production were apparent. In vascular plants, morphological changes in plant height and other parameters may occur under enhanced UV-B radiation without any decrease in plant productivity (e.g. Barnes *et al*. 1990; 1995). Such morphological changes have been suggested to be mediated by phytochrome or a specific UV-B photoreceptor (as reviewed by Caldwell *et al*. 1999). A similar explanation may be relevant for *Sphagnum*, although there has been little study of the UV photobiology of mosses. The decrease in volumetric density of *S. magellanicum* in our study does not appear to be related to stem density (i.e. number of stems per unit area remained constant) and changes in leaf mass on individual stems of *S. magellanicum* may be of more importance.

In this *Sphagnum* peatland, morphology of the three vascular plant species tended not to respond to solar UV-B reduction. *Tetroncium magellanicum* showed some indication of increased leaf elongation under reduced UV-B relative to near-ambient UV-B conditions during the second and third growing seasons, but the results were not statistically significant at $P = 0.05$. In New Zealand, seedling height of *Nothofagus solandri* increased and the number of leaves decreased with solar UV-B exclusion when these potted seedlings were well fertilized (Hunt & McNeil 1999). *Nothofagus antarctica* may not have responded to UV-B reduction in our study because it is severely stunted by harsh conditions such as low pH and nutrient limitation. Other environmental stresses most often appear to dampen the response to UV-B radiation (as reviewed by Caldwell & Flint 1994). Stem elongation of *Empetrum rubrum* did not respond to three growing seasons of UV-B reduction, although a previous study using UV-B enhancement did find a large (33%) reduction in *E. hermaphroditum* after only 2 years at Abisko, Sweden (Johanson *et al*. 1995). Further studies over 7 years with *Empetrum hermaphroditum* and other dwarf shrubs at Abisko have shown few effects of enhanced UV-B on plant growth, although some interactions with increased summer precipitation were apparent (Gwynn-Jones *et al*. 1997; Phoenix *et al*. 2001). These results for *Nothofagus* and *Empetrum* indicate that UV-B effects may occur only under specific site conditions and for certain species.

A parallel study in Tierra del Fuego has shown that subtle changes in plant morphology due to solar UV-B manipulation were more common at a shrub-steppe site than in the *Sphagnum* peatlands (Rousseaux *et al*. 2001). The leaf or frond length of the herbaceous species *Gunnera magellanica* and *Blechnum penna-marina* was consistently 5–10% greater under reduced solar UV-B, while the woody evergreen shrub (*Chiliotrichum diffusum*) was unaffected. In Antarctica, similar solar UV-B reduction experiments using plastic filters increased leaf elongation rates by over 40% after 4 years in the tussock grass *Deschampsia antarctica* and increased leaf number in the cushion plant *Colobanthus quitensis* by 25% (Day *et al*. 2001). The larger plant responses to solar UV-B manipulation in Antarctica than in Tierra del Fuego have been suggested to be related to the much more pronounced ozone depletion over Antarctica (Ballaré *et al*. 2001).

The UV-B-absorbing compounds (i.e. flavonoids and other phenolics) in plants are considered to be potentially important protective compounds against UV-B radiation. Cell wall-bound phenolics in the genus *Sphagnum* contribute greatly to the resistance of *Sphagnum* material to decomposition (Verhoeven & Liefveld 1997). In Tierra del Fuego peatlands, these phenolics may stay bound in the leaves of *S. magellanicum* for several years (Searles, unpublished data). The interaction found in this study between UV-B and year for UV-B-absorbing compounds may suggest that *S. magellanicum* is slowly responding to solar UV-B reduction, or that a response only occurs under certain climatic conditions. Any change in phenolics may be important for the decomposition of recalcitrant *Sphagnum* peat over decades. The 10–20% decrease in UV-B-absorbing compounds in *T. magellanicum* under

reduced solar UV-B is similar in magnitude to the response of many vascular plant species from other systems to solar UV-B exclusion (e.g. Hunt & McNeil 1999; Xiong & Day 2001). However, in a parallel experiment in Tierra del Fuego, the level of UV-B-absorbing compounds of three species in a shrub-dominated community tended not to respond to UV-B reduction (Rousseaux *et al*. 2001) nor did *Vaccinium* shrub species demonstrate a change in UV-B absorbing compounds under enhanced UV-B in Abisko, Sweden (Phoenix *et al*. 2000).

POTENTIAL ECOSYSTEM CONSEQUENCES

Although some growth responses were apparent after 3 years of solar UV-B manipulations in *S. magellanicum*, and to a lesser degree in the vascular plants, the community- and ecosystem-level consequences of these responses are still not certain. The lesser height growth of the moss under near-ambient than under reduced UV-B may benefit the vascular plants over the long-term if the rate of moss growth over vascular plant tissue is decreased. The race, albeit slow-paced, between the growth of *Sphagnum* and the emergent vascular plants determines the plant community composition of this system. Thus, even slight differences in UV-B effects on height growth of the moss and the vascular plants may be of importance.

The role of trophic interactions as important components of ecosystem response to an altered UV-B climate has been stressed by Bothwell *et al*. (1994) and Paul *et al*. (1997). For example, solar UV-B reduction affected components of the microfaunal and microfloral communities of the *Sphagnum* peatland. The number of testate amoebae inhabiting the *S. magellanicum* capitulum were greater under near-ambient UV-B than reduced UV-B in each of the three growing seasons, while leaf fungi on *N. antarctica* were less common on the upper leaf surfaces under near-ambient UV-B (Searles *et al*. 1999; Searles *et al*. 2001). Also, insect herbivory on the perennial herb *Gunnera magellanica* in the shrub-steppe community was greatly decreased under near-ambient UV-B during the austral spring when solar UV-B levels are most affected by the Antarctic 'ozone hole' (Rousseaux *et al*. 1998; Rousseaux *et al*. 2001). The overall response to UV-B in many ecosystems may be a complex combination of UV-B responses involving vegetation, other trophic levels such as microbes and insects, and the interactions between these organisms. Ultraviolet-B effects on vegetation appear to be modest, based on the results from our experiments. Nevertheless, substantial recovery of the ozone layer is not expected until the middle of this century even under optimistic scenarios (World Meteorological Organization 1999). Thus, even modest effects on vegetation and the often more pronounced effects on organisms in other trophic levels may accumulate over the considerable time periods anticipated before ozone recovery.

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